# CHANGES IN SHAPE WITH TIME IN AUSTRALIAN SPECIES OF AUCELLINA POMPECKJ (AVICULOPECTINIDAE)

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(Text Fig. 1-7.)

#### ABSTRACT.

Progressive changes in shape and size with time of right valves of a series of forms of *Aucellina* Pompeckj, the best known of which is *Aucellina hughendenensis* (Etheridge sen.), are demonstrated. The presumably genetically controlled variations took place during upper Albian times, i.e., during the time of deposition of what is known as the Tambo Formation of the Great Australian Artesian Basin. Systematic position and phylogeny of Aucellininae *nov.* are discussed.

#### INTRODUCTION.

The individual elements of the marine faunas contained in the Lower and Middle Cretaceous formations of the Great Australian Artesian Basin are fairly well known from numerous publications by pioneers of Australian Mesozoic palaeontology such as W. B. Clarke, R. Etheridge sen., R. Etheridge jun., W. H. Hudleston, F. McCoy, C. Moore, J. E. T. Woods, F. W. Whitehouse, and some others. A very important aspect of the biostratigraphy of the eastern Australian Cretaceous, however, is still in its infancy. It is the establishment and delimitation of local faunizones, their correlation with each other, and their relation with standard zones overseas.

The first serious attempt to subdivide the Cretaceous System of the Artesian Basin according to faunizone concepts was made by Whitehouse (1926a, 1926b, 1927, 1928). Through an admirable analysis of all then known ammonites he established which of the standard zones of the Aptian and Albian Stages are likely to be represented in the Artesian Basin formations provided always, of course, that the succession of species responsible for the European standard time-scale can be assumed to repeat itself in the form of more or less closely related, analogous, form series in Australia.

Broadly speaking, the assumption of such repetition is part of the fundamental working hypothesis applied to palaeontological-stratigraphical correlation problems. However, the early and rather uncritical enthusiasm for this hypothesis has in the last two or three decades been somewhat dampened. While it still holds good in principle, it has also become evident that the concept had been driven too far when it was assumed that any, even the smallest, subdivision of a faunizonal time-scale was a world-wide recognizable thing.

Whitehouse (*loci cit.*) was working under a significant handicap. Although he described and analysed a great number of ammonites from various collections, he had little or no exact information on and could therefore not vouch for their relative position within the formations whence they came from. He was able to show, e.g., that genera and species, which, in Europe, are found together in a certain zone, have

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their phenotypical counterparts in a formation of the Artesian Basin sequence. Yet there does not *eo ipso* follow that the Australian forms are contemporaneous in the same way as are their European cousins. In the absence of direct field evidence Whitehouse simply had to assume that this is so. This may well be correct, of course, but to this date Whitehouse's zonal subdivision of the eastern Australian Cretaceous has not been factually substantiated and remains a working hypothesis the applicability of which must still be demonstrated.

This paper is a small step in a similar, or parallel, direction. By the example of *Aucellina* is shown what interesting results may be obtained from the study of faunas encountered in continuous bore cores. Thousands of bores have, of course, been drilled in the Artesian Basin in order to tap the vast water resources it contains. Unfortunately, the great majority of these bores were sunk with percussion (cable) tools. There are consequently scarcely any worthwhile records of macrofossils in the respective logs. Even from the limited number of bores in which cores were taken one knows preciously little about the sequence of fossils in the formations that have been penetrated.

The continuously cored bore which yielded the hereafter described series of Aucellina forms was drilled in 1957 by an oil company a few miles north-west of Oodnadatta, in northern South Australia, i.e., in the western marginal region of the Great Artesian Basin. To my knowledge it is the first continuous bore section whose succession of marine Cretaceous faunas has been recorded in detail while drilling was in progress. Not unexpectedly, I found a number of characteristic genera and species to be restricted to certain levels within the formations, but this short paper is not the place in which to enlarge on these interesting and important observations which have opened promising new avenues for more accurate and useful local zoning of the Cretaceous System in Eastern Australia.

For the present state of our knowledge on the stratigraphy and structure of the Great Artesian Basin the reader is referred to the up-to-date summaries by Sprigg (1958), Sprigg and Staff (1958), Whitehouse (1954), and David (1950). In Sprigg and Staff (1958) a summary log of the Oodnadatta bore (fig. 19a, p. 92) and an account of the recent stratigraphical observations (pp. 94-97, Rolling Downs Group) is given. Our *Aucellina* form series is from the "richly fossiliferous mudstone (Tambo Formation)" which comprises the top 425 ft. of the bore section. The individual members of the form series were found at the following levels:

#### Table 1.

Ranges of Aucellina Species in Bore near Oodnadatta,

Form F (youngest) was found on surface, probably in beds which are slightly younger than the beds of the top part of the bore section.

- Form E, approximately from depth 100 ft. to 0 ft.
- Form D, approximately from depth 235 ft. to 220 ft.
- Form C, approximately from depth 300 ft. to 240 ft.
- Form B, approximately from depth 345 ft. to 250 ft.
- Form A, approximately from depth 375 ft. to 330 ft. (oldest).

All specimens described hereafter are deposited in the palaeontological reference collection of the consulting firm Geosurveys of Australia Ltd., Grenfell Street, Adelaide.

### ON THE SYSTEMATIC POSITION OF AUCELLINA POMPECKJ.

The genus Aucellina was introduced by Pompeckj (1901) in order to accommodate a number of Middle Cretaceous (Aptian to Cenomanian) Aucella-like lamellibranchs which are known from various parts of the world. Of the two typical species named by Pompeckj Aucellina gryphaeoides (Sowerby) was subsequently designated as genotype by Marwick (1939).

The question of the systematic position of the genera Aucella Keyserling<sup>1</sup> and Aucellina has been the cause of much discussion among taxonomists. An exhaustive analysis is found in Pompeckj (1901). Although he did not really solve the problem his meticulous description and comparisons of the morphological features and those of related genera came to be the foundation of all later discussions. It seems the problem has recently been solved for good. Ichikawa (1958) demonstrates convincingly that Aucella and Aucellina belong to the family Aviculopectinidae (Etheridge jun., 1906) em. Newell, 1938, in which he has grouped them as subfamily Aucellinae (Fischer, 1887) em. Ichikawa, 1958, along with Oxytominae Ichikawa, 1958; Aviculopectininae Newell, 1938.

Whether Aucellina and Aucella should be regarded as members of the same subfamily may be of secondary importance, but nevertheless questionable. As Pompeckj (1901) has clearly shown, they are not as closely related as their superficial similarity in outline and other characters suggest. Their hinge features are evidently not the same. In Aucella there is a rather high degree of what may be called specialization when compared with the hinge features in the ancestral lineage which, as Ichikawa (1958) suggests-as did Pompeckj-includes Pseudomonotis Beyrich, 1862, and Meleagrinella, Whitfield, 1902. Aucellina, on the other hand, has hinge characters which are in every respect closer to the ancestral Meleagrinella (= Pseudomonotis in Pompeckj, 1901) pattern than to that of Aucella. The latter is not likely to have been the forerunner of Aucellina except, of course, in the sense that the aucellid phenotype had evolved from meleagrinellid stock once before, i.e., in Upper Jurassic times. By the end of the Neocomian this specialized lineage had, however, died out, and Aucellina evolved during the Aptian independently, again showing clearly the ancestral hinge characters of Meleagrinella, i.e., characters which all later species of Aucella had largely lost. There is no evidence of intermediate forms which would link the specialized late forms of Aucella with the earliest representatives of Aucellina. Pompeckj (1901) has demonstrated this point, and since then nothing has been discovered that would contradict his findings. On the other hand, since the genus Meleagrinella-which has its earliest representatives in the Rhetian (Ichikawa 1958)-persists together with Oxytoma Meek, 1864, into the Upper Cretaceous, Aucellina could easily have been an offshoot in the Lower Cretaceous from that stock, as was Aucella at the beginning of the Upper Jurassic.

<sup>1</sup>As regards the case Aucella versus Buchia Rouillier, 1845, see Jeletzky (1955).

The Aucellina lineage thus forms a phylogenetic group of equal rank as does the Aucella series or, for that matter, the predominantly Australian series of Maccoyella Etheridge jun., 1892, which stems also from aviculopectinid stock and arose at about the same time as did Aucellina. Phylogenetically this should be expressed by accommodating Aucella and Aucellina in separate subfamilies, i.e., Aucellinae (Fischer, 1887) em. Ichikawa 1958, and Aucellininae nov. of the Aviculopectinidae.

### THE AUSTRALIAN REPRESENTATIVES OF AUCELLINA.

Species of Aucellina are among the commonest forms in eastern and northern Australian Albian formations. Because of the sessile and gregarious habits of the genus, one finds in places bands of real Aucellina-coquinites. The earliest Australian record is found in Etheridge sen. (1872) under the name Avicula hughendenensis. Etheridge jun. (1884) transferred this species to Aucella, and Pompeckj (1901) finally to Aucellina.

Pompeckj (1901) records, ap art from A. hughendenensis, also A. gryphaeoides (Sowerby) from the Albian of Queensland. The species from the uppermost Albian near Darwin (Whitehouse, 1926b) received the name A. incurva by Etheridge jun. (1902). All three forms are similar morphologically, but they cannot be taken as variations of the one species, e.g., of A. gryphaeoides, as has been suggested to me verbally by colleagues. A. incurva is, on closer inspection, quite distinct from A. gryphaeoides. The latter's left valve has a far less prominent umbo, and its right valve shows not only a relatively larger anterior ear and a correspondingly narrower byssus slit, but also a fairly large posterior ear (or wing), a feature that is almost non-existent on A. incurva. Excellent figures of A. gryphaeoides are given in Woods (1905, pl. 10, figs 6-13).

Actually, the right valve of *A. incurva* is more like that of *A. aptiensis* (d'Orbigny), i.e., more or less obliquely circular (see Pompeckj, 1901, pl. 16, figs. 1-4). But these two species differ decidedly in the form of the left valve.

Closest to A. gryphaeoides is evidently Etheridge's A. hughendenensis. The only difference between these two lies in the latter's distinct radial riblets and striae on the left valve (in addition to the concentric ornament) and the typically more elongate, fan-like, obliquity of its right valve. On A. gryphaeoides radial ornamental elements are only rarely noticeable, and then on right valves and only very faintly. The crnament of A. hughendenensis recalls more that of A. sancta-quirini Pompeckj, but the latter's left valve has a slenderer and higher umbo and is in general outline more elongate oblique and slender, i.e., similar to A. incurva.

Consequently, it is better to keep the mentioned Australian species separate from each other and from overseas representatives of Aucellina, at least at the present stage of our knowledge of these forms. As will be seen presently, there is a fair measure of justification for such a cautious approach because the analysis of the Aucellina series from Oodnadatta suggests strongly that these and other forms are representing stages in a phylogenetic lineage. They are not geographical variations or subspecies, not "Standortsrassen" (local races of a species). These stages evolved through long times (several millions of years); when stage 3, for example, had been reached there were evidently no survivors left of stage 1. None of stage 2 were left when stages 4 or 5 were flourishing, and so on. Wright (1958) has recently again emphasized the point of view of the palacontologist as regards the concept of "species." The current definition of species as "a potentially interbreeding population" is rather wide open to criticism in its application to classification. It is a neontologist's concept which ignores the element of time. In the case of the *Aucellina* series, as in many other cases, we have no means of testing whether the early and late stages could interbreed. Placing all known Australian forms into one and the same species would, however, imply just that. This is surely a much too venturesome assumption. Consequently, as long as the evolutionary stages are in some or other way recognizeable and separable morphologically they should be treated as distinct species. In the following demonstration of an *Aucellina* series this principle is adhered to, although—because of the still rather small number of specimens available—a nomenclatura aperta is applied.

### THE AUCELLINA SERIES FROM OODNADATTA.

Six morphologically distinguishable types of right valves are now known from the Albian of northern South Australia. Left valves show, apart from size, scarcely any differences. If there are some, they have probably been obliterated by the effects of rock diagenesis. Aucellina, unlike many species of Aucella, is very thin-shelled and fragile. Left valves especially, being much more inflated than right valves, are always found crushed with their delicately twisted umbo flattened and the hinge characters distorted. The primarily flattish right valves, however, are commonly perfectly preserved and can be studied in every detail. They are shown in text fig. 1-6 along with the necessary descriptions.

### AUCELLINA sp. nov. A. aff. A. APTIENSIS (d'Orbigny).

## Text fig. 1, (x 1½).



Aucellina sp.nov. A. aff. A. aptiensis (d'Orbigny). Right valve, side and frontal aspects.

Description: A small species of the series. This right valve is moderately inflated, with rather distinct, slightly opisthocline (see Newell, 1938) umbo. Height and length are equal. Both anterior and ventral margins are evenly rounded. Posterior margin straight, forming an angle of between  $90^{\circ}$  and  $100^{\circ}$  with the cardinal margin, thereby enclosing an almost recto-triangular, clearly individualized, posterior ear (or area).

The anterior ear (or byssus ear) is long and slender. It is turned upward at an angle of  $20-25^{\circ}$  to the cardinal margin, as well as inward, i.e., against the left valve. The byssus slit between it and the prominently produced antero-cardinal wing (or ear) is wide and deep, reaching almost beneath the umbo.

The ornament consists of both radial and concentric striae and riblets. The radial ornament weakens towards the ventral and the posterior margins. Only concentric striae remain there. Fine concentric lamellae are discernible also on the byssus ear.

Comparisons: This right valve does not match any of the species described in the literature. None of these shows the up-and-inward twisted byssus ear and the subrectangular postero-cardinal margin. In its other features, especially the opisthoclinal to aclinal umbo, *sp. nov.* A. recalls to some extent *Aucellina aptiensis*. This is perhaps not surprising because the Australian form is, like d'Orbigny's species, apparently the oldest of a phylogenetic series. It certainly differs very much from *A. hughendenensis*.

The figured specimen comes from a depth of 370 ft. 8 in. in the bore. The vertical range of the species is given in Table 1.

AUCELLINA sp. nov. B. cf. A. GRYPHAEOIDES (Sowerby).

### Text fig 2, (x 1½).



### Aucellina sp. nov. B cf. A. gryphaeoides (Sowerby).

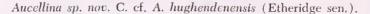
Right valve, side and frontal aspects.

Description: A small species of the series. This right valve is moderately inflated, with rather distinct, acline to slightly prosocline umbo. Height and length are equal. Anterior and ventral margins evenly rounded. Posterior margin straight, forming an angle of 115-125° with the cardinal margin, thereby enclosing a clearly individualized posterior ear. The anterior or byssus ear is fairly long, but not as slender as in the other forms. It is turned upward at an angle of 10-20° to the cardinal margin, as well as slightly inward towards the left valve. The byssus slit is wide and deep, reaching beneath the umbo. The antero-cardinal wing is produced with a sharply curved margin. The ornament consists of both radial and concentric striae and riblets. The radial elements weaken towards the ventral and the posterior margins, where only concentric striae and weak folds remain. The concentric (transverse) lamellae on the byssus ear are very weak.

Comparisons: This form is very similar to sp. nov. A, but has a less up-and-inward twisted byssus ear, a greater postero-cardinal angle, a less dense radial ornament, and a nearly horizontally (instead of upward) opening byssus slit. Also, the antero-cardinal edge is less upward produced than in sp. nov. A. With its prosocline umbo and the consequent tendency to the typical aucellinid obliquity sp. nov. B begins to approach the phenotype of Aucellina gryphaeoides (see Woods, 1905, pl. 10, figs. 6c and 7b) although its postero-cardinal angle has not yet reached the obtusity of the respective European species. In this it also differs from A.  $hugh e_{1,c}$ , denensis, whose elongate obliquity of the right value is (as in A.  $grypha_{1,c}$ , oides) much more pronounced.

The figured specimen comes from a depth of 298 ft. 6 in. in  $th_e$  bore. For the vertical range of the species see Table 1.

AUCELLINA sp. nov. C. cf. A. HUGHENDENENSIS (Etheridge sen.). Text fig 3, (x 1½).



Right valve, side and frontal aspects.

Description: A medium to fairly large sized species of the series. Right valve almost flat, with scarcely protruding acline to prosocline umbo. Length exceeding height by about 10%. Anterior and ventral margins evenly rounded. Posterior margin first continuing as evenly convex as the ventral margin but towards the cardinal margin developing a slightly concave re-entrant. The posterior ear is thereby well individualized. The postero-cardinal angle is typically well over  $120^{\circ}$ . In outline this species is therefore nearly circular with a long, straight, cardinal margin. The byssus ear is long and slender, forming a horizontal process that is *not* twisted against the left valve. The byssus slit is long and narrow, reaching to the small umbo. The antero-cardinal wing of the valve has a horizontal, straight, cardinal margin (almost as long and straight as the posterior cardinal margin), which curves gently into the anterior margin.

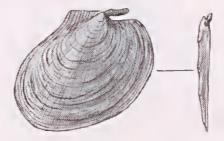
The ornament of concentric striae and weak folds is rather attenuated, and so are the fine lamellae on the byssus ear.

Comparisons: The flatness of the valve, the features of the cardinal margin, the slight concavity of the upper posterior margin, and the increased average size as well as the height/length ratio of this sp. nov. C quite definitely foreshadow Aucellina hughendenensis. Yet it is equally obvious that sp. nov. C has not quite "arrived" there. Its only slightly prosocline umbo and consequently little oblique, almost circular, outline still recalls the forerunners A and B sp. nov. C is also individualized by the complete absence of radial elements in its ornament of the right valve. This characteristic feature may actually mean that A. hughendenensis proper, with its typical radial ornament, is an independent offshoot from A or B, i.e., that sp. nov. C is not in its ancestral stock.

The figured specimen comes from a depth of 296' 4" in the bore, and the vertical range of the form is shown in Table 1.

#### AUCELLINA HUGHENDENENSIS (Etheridge sen.)<sup>2</sup>

Text fig. 4 (x 1½).



Aucellina hughendenensis (Etheridge sen.) Right valve, side and frontal aspects. 2 = Form D on Table 1.

Description: This well-known species belongs to the largest that have been evolved within the genus. The right valve is almost flat, with a very small umbo which is moderately to strongly prosocline. Length exceeding height by over 10%. Anterior and ventral margins broadly and evenly rounded. Posterior margin evenly convex in lower part but fairly strongly concave before reaching the cardinal margin, thereby deliminating a rather long, obtusely triangular posterior ear. Posterocardinal angle 130-140° or even more. In outline this species is therefore fairly elongate oblique with a moderately long, straight, cardinal margin (about half the length of the valve). Except for being shorter in relation to the length of the valve, the features of the cardinal region are almost identical with those in *sp. nov. C.* Because of a slenderer byssus ear, however, the byssus slit appears somewhat wider.

The ornament consists of both radial and concentric elements. There are dense radial striae and fairly broad, but low, concentric folds. The concentric striae are of about equal density as the radials except on the posterior, marginal portion of the valve, where only concentric elements remain. Byssus ear finely lamellate.

Comparisons: The affinities of Aucellina hughendenensis have been discussed in the introductionary parts to this article. In our series it stands, morphologically speaking, between A/B on the one hand and C/E/F on the other, i.e., by uniting and carrying characteristic features of the two other groups it may be taken as "typifying" the whole series in its "temporal and geographical variation," and as far as Australia is concerned, in the sense of Wright (1958, p. 144, para. 2).

In itself, however, A.hughendenensis is probably a single offshoot from the main line (which was carried on through E and F to A.incurva, while hughendenensis died out before incurva appeared) that was very successful for a short time but left no descendants.

The typical A.hughendenensis as represented by text fig. 4 occupies only a small interval of Albian times. The figured specimen comes from a depth of 231' in the bore. The apparently very short range of the species is shown on Table 1. AUCELLINA sp. nov. E. cf. A. INCURVA (Etheridge jun.). Text fig. 5, (x 1½),



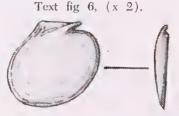
Aucellina sp. nov. E. cf. A. incurva (Etheridge jun.). Right valve, side and frontal aspects.

Description: This species is of moderate to large size. The right valve is only very slightly inflated. The only moderately prosocline umbo is small but well defined, sharply pointed, and protruding a little above the cardinal margin. Height of valve only slightly less than length. Posterior, ventral, and anterior margins evenly rounded. Antero-cardinal edge sharply rounded, almost angular. Posterior wing small and rounded, forming only a narrow, elongate area behind the umbo. Byssus ear slender, fairly long, horizontal. Byssal slit deep and narrow, reaching beneath the umbo. Anterior cardinal margin long, a little concave, about twice as long as the byssal ear. Anterior wing of valve prominently extended, relatively much larger than in any of the other forms. In outline this form is thus subcircular, but conspicuously in quilateral with the umbo set backward. The cardinal margin as a whole is long (about <sup>2</sup>/<sub>3</sub> the length) and slightly concave, without the typical en-échélon step-down under the umbo (in side view) of the other species. Byssus ear parallel to cardinal margin, not twisted towards left valve. Ornament of extremely fine concentric striae or none at all. Very fine lamellae on byssus ear.

Comparisons: This species clearly approaches Aucellina incurva especially in its enlarged anterior wing and the loss of the angularity of the postero-cardinal edge. However, because of its well-defined umbo and its subcircular rather than obliquely elongate outline it remains distinct from A.incurva (Etheridge jun., 1902, pl. 7, figs. 22, 24, 27).

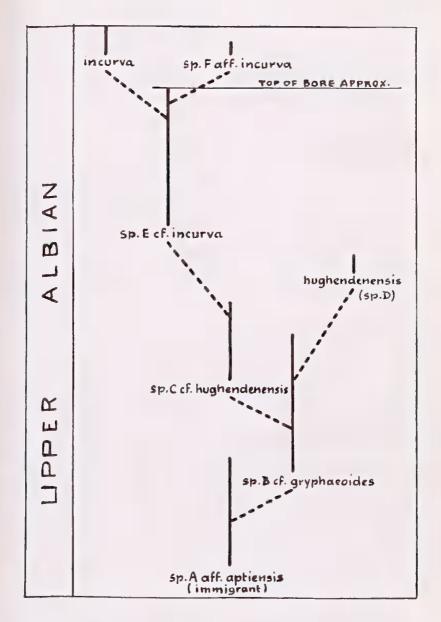
The figured specimen comes from a depth of 73' 5" in the bore. The range of the species is shown on Table 1.

AUCELLINA, sp. nov. F aff. A. INCURVA (Etheridge jun.)



Aucellina sp. nov. F. aff. A. incurva (Etheridge jun.). Right valve, side view.

*Description*: This is a small species of the series. The right valve is flat or only slightly inflated. The poorly defined umbo is strongly





# PHYLOGENY OF AUSTRALIAN AUCELLININAE.

Note: Branching to the right means tendency towards phenotype of Aucellina hughendenensis. Branching to the left means tendency towards phenotype of Aucellina incurva prosocline. Height of valve only slightly less than length. Anteriot and ventral margin broadly and evenly rounded, posterior margin straight or faintly concave towards cardinal margin, forming an obtuse angle (over  $130^{\circ}$ ) with the latter and thereby enclosing an elongate, narrow, triangular posterior ear similar to that in *sp. nov.* C. Byssus ear short, more like a simple, sharp fold than a spoon-shaped process. Byssal slit rathet short and narrow. Anterior wing of valve rather small with evenlys broadly rounded antero-cardinal end. Posterior portion of shell conspicuously larger than anterior, umbo set forward. In outline this form js therefore moderately elongate oblique. No ornament noticeable.

Comparisons: Since this form was found on the surface in a quite different state of preservation (limonite replacement) from those in the bore comparison is not easy. In general outline it resembles Aucellind hughendenensis, but the short and simple byssus ear and the absence of any ornament may indicate closer relationships to the species E and C, i.e. to the lineage which seems to end in A.incurva. The exact stratigraphical position of this form F is unfortunately not known, but it is certain that it is younger than species E not only because F was not encountered in the bore, but also because field evidence suggests that the gypsiferous beds which contain F are probably younger than the youngest beds in the bore. These circumstances prompt me to leave sp. nov. F. in the incurva group.

The figured specimen comes from the gypsiferous shales just north of the Arckaringa Road about fifteen miles south-west of Oodnadatta,

#### SUMMARY AND CONCLUSIONS.

The afore described six species of Aucellina, in this case all characterised by the features of their right valves under nomenclatura aperta, show that variations in shape and size with time are very considerable in this genus even within a comparatively short geological time interval such as the upper Albian. It is understood, of course, that additional drilling in the Artesian Basin may not only bring about some corrections to the range in time of the individual members of this Aucellina series, but may also produce a number of intermediate forms which may appear to close some of the as yet quite astounding "gaps" between our six species. Yet this cannot alter the fact that rapid phenotypic changes take place on what I consider to be the specific level. The discovery of some more Aucellina forms could possibly make the taxonomic classification of the members of this series more difficult because transitional forms might have to be accommodated. Yet this may not prove to be problematical.

It all depends at what time such "transitional forms" make their first appearance. A form which appears morphologically intermediate between e.g. our species A and B will spell taxonomic trouble for A and B only if its first appearance is before or, at the latest, at the same time as that of B, i.e., if the new form is transitional also in the temporal sense. If it appears after B, however, or even after C or D, it must be classified as a separate species. It is most likely a homoeomorph, a throw-back, further along the lineage, which means that it had no chance of interbreeding with the phenotypically similar ancestors—the latter were already extinct. The "transitional form" must stand on its own in such cases. This is also, I presume, what Wright (1958) means by "phylogenetical thinking," and I cannot but agree with him. One understands why he repeatedly criticised neontologists for some of their classification efforts which did not allow for the element of time.

To conclude this paper on the Australian *Aucellina* series, the results are presented in text fig. 7 in the form, still tentative, of course, of a phylogenetic interpretation.

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